AVIAN PREDATION ON IMMATURE STAGES OF THE LOCUST BORER, *MEGACYLLENE ROBINIAE* (FORSTER) (COLEOPTERA: CERAMBYCIDAE)

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Abstract.—Avian predation on the locust borer, *Megacyllene robiniae* (Forster), was studied in 15 black locust *(Robinia pseudoacacia* Linnaeus) stands in western Maryland during 1987–88. Only woodpeckers were observed in the act of predation, but other avian species could not be discounted in assessment of past predation. The overall predation rate was low, ranging from just 0–1.7%, except in one stand where birds depredated 20% of the borers over a 2-year period. Birds focused their attacks on late instar larvae and pupae, the largest life stages. There was no evidence of predation on the much smaller, overwintering first instar larvae. Intensity of predation was related directly to larval and, especially, pupal density. Predation was more common in relatively small, unhealthy trees and in small trunks and branches. Most predation was attributed to hairy woodpeckers *(Picoides villosus* Linnaeus), based in part on direct observations and excavation characteristics. The overall low predation was likely due to a complex of factors that limited numerical and functional predatory responses to locust borers, including predator terri torial behavior and seasonal shifts in foraging patterns, relatively low borer density, and black locust tree characteristics that could impede foraging (e.g., large thorns).

Key Words: black locust, excavations, tunnels, woodpeckers

Woodpeckers have long been regarded as important predators of wood-borers (Beal 1911, Forbush 1927, Bent 1939), a complex of insects that tunnel in the sapwood and heartwood of live trees and account for sub stantial annual timber losses in the eastern United States (Donley and Worley 1976, Nielson 1981). Recent research has ad dressed biological aspects of potential wood-borer predators, particularly the red cockaded woodpecker *(Picoides borealis* Vieillot), including foraging behavior (Engstrom and Sanders 1997, Doster and James 1998), competition (Knapps 1997, Saenz et al. 1998), habitat (Engstrom and Mikusinski 1998), and arthropod prey (Hanula and Fanzreb 1995). For pileated woodpeckers *(Dryocopus pileatus* Linnae us), studies of habitat preferences have in dicated importance of large trees and snags (Renken and Wiggers 1993), whereas oth ers have dealt with interspecific competition in which pileated woodpeckers enlarged nesting cavities of red-cockaded woodpeck ers (Saenz et al. 1998), and intra-specific competition between pileated woodpecker males (Oberman 1995). Although consid erable research has been has been devoted to the role of birds in regulating insect pop ulations (e.g., Knight 1958, Otvos 1965, Dickson et al. 1979, Cooper and Smith 1995), few studies have documented the

impact of birds on populations of wood-borers, or longhorned beetles, of the family Cerambycidae, and little information is available on factors that influence the rate of predation. In this paper, we describe avian predation, believed to be mostly by woodpeckers, on the locust borer, *Megacyllene robiniae* (Forster), a common woodborer invading the black locust tree *Robinia pseudoacacia* Linnaeus. In heavily-infested black locust stands in Ohio, Hall (1942) considered woodpeckers to be the most effective predator, but presented no data. Our objectives were to determine the rate and phenology of predation and examine possible relationships between the incidence of avian attacks and borer density, tree characteristics, and the within-tree location of borers.

The locust borer is a primary (i.e., invades only living trees), monophagous (consumes only one host species), univoltine (1 generation per year), wood-boring species that is native throughout much of the natural range of black locust (Hall 1942, Galford 1970). The egg, larval, and pupal stages reside in the live branches and trunks of black locust trees. Eggs are laid singly in bark crevices during August through early October. Hatching occurs from 8 through 10 days following oviposition. The first instars bore into the inner bark where they overwinter in small (4–5 mm diameter) oval galleries. Larval activity first becomes evident the following spring when they resume feeding, resulting in an accumulation of frass, wood dust, and sap along the bark surface just outside the excavation entrance. As the larval activity continues during early through mid-summer, their tunnels extend into the sapwood and heartwood. Tunnel access to the outside is maintained throughout this period, and scars with various configurations may form only after adult emergence (Harman and Dixon 1984). A completed borer mine ranges from 10–21 cm long, 5–8 mm in diameter and extends 1–6 cm deep into the wood. The mine typically resembles a twisted, inverted "J" and is oc-

cupied by a single larva. Cavities are usually excavated beneath the outer bark by the borer larvae in their early instars, as they begin feeding, prior to construction of tunnels. These vary in size to as deep as 1 cm, and as wide as 2 cm, and may harbor an array of inquiline invertebrate species (Larson and Harman 2003). When fully developed, larvae measure 20–30 mm long and 5–7 mm in diameter. Pupation occurs during mid-July through August and adults emerge in August through early September. Detailed accounts of the locust borer life cycle are provided by Hall (1942) and Galford (1970).

MATERIALS AND METHODS

This study was conducted in 15 black locust stands in western Maryland, near the Allegheny Ridge, in the central Appalachian Mountains. Stands were located at elevations ranging from 582 through 850 m, and all were of intermediate age (20–40 yrs). The landscape is dominated by oak, hickory, and northern hardwood forests interspersed with small farming communities and coal strip-mined areas.

To examine predation in a variety of habitats, we selected three stands in each of the following five site categories: (1) old field, (2) pasture, (3) forest opening, (4) roadside, and (5) reclaimed strip-mines. Each stand contained a natural (not planted or seeded) sere or progression of black locust growth that extended outward from mixed-species forest, 200 ha or larger, into an adjacent open area (e.g., an old field or reclaimed strip-mine). The seres comprised as many as five discrete, easily identifiable black locust successional stages: mixed forest, forest-clone edge, clonal black locust growth, clone-open edge, and open growth. Detailed descriptions of the vegetation in each successional stage are provided by McCann and Harman (1990) and McCann (1992). The above site categories were chosen because they were most representative of growth situations for black locust in the region.

Data collection.—During 1987, preda tion rate was estimated by determining the percentage of active borer mines that were depredated on the bottom 3 m of 10 ran domly selected trees (herein referred to as sample trees) per successional stage per stand. Thus, as many as 50 sample trees per stand (total 489) were monitored for pre dation. In some stands, reduced sample siz es were necessary because certain succes sional stages were absent or fewer than 10 black locust trees per successional stage were present. Sample trees were selected using a modified point-quarter method (Cottam and Curtis 1956). This method in volved establishing line transects at 8 m in tervals perpendicular to the forest edge. At random points along the transects, the near est black locust tree was chosen from a ran domly selected 90° quadrant.

Active borer mines were tallied on the bottom 3 m of each sample tree during May. Larval tunneling was identified by presence of fresh sap, frass, and wood dust exhuding from entrance holes. Each mine was marked with crayon by placing a small dot on the bark within 3–6 cm of its en trance. Sample trees were then checked for predation once per month during May through Sept. A mine was considered probed by a predator if an excavation (e.g., a conical hole or chipped bark) was present within 5 cm of the mine entrance. Occa sionally, identity of the prey item was un certain and a knife was used to cut into the wood to verify the presence of an active locust borer mine.

Data collected for each sample tree in cluded diameter at breast height (dbh), tree height, and crown class. Crown class des ignations were: dominant, codominant, in termediate, or suppressed (Smith 1962). Data collected for each active borer mine included height above ground, stem diam eter, orientation of entrance (north vs. south), and branch versus main bole. In in stances of predation, length, width and depth of the predatory excavation were measured. Also recorded was whether the

predator entry was typical of a woodpecker species; remaining entries were considered birds of unknown species. To determine whether the borer evaded predation and sur vived to the adult stage, wire screen traps (3.1×3.1 mm mesh) were stapled over the emergence hole to capture any emerging adults. Traps were in place during during July through September, and were then checked for emerged adults every 7–10 days. In addition to the above, trunk sur faces of all trees in each stand were inspect ed for signs of predation to a height of 12 m, using 10×50 binoculars, an 8- m ex tension ladder or a modified rock-climbing method (Perry 1978). These surveys in cluded counts of borer tunnels from previ ous as well as current year, and allowed us to (1) obtain additional information on pre dation characteristics, (2) qualitatively judge the validity of predation rate esti mates, and (3) help determine if predation occurred during the overwintering stage (October through April). Complete stand surveys were conducted monthly during May through September and tri-monthly during October through April. During the winter surveys, any excavation found in trunks or branches was considered potential predation because young larvae show no external evidence of their presence until at least late April. If predation was suspected, the bark area surrounding the excavation was exposed with a knife to confirm the presence of a locust borer hibernaculum.

In one of the 15 stands (RD3) where the predation rate was relatively high, predation was monitored an additional year and pre dation characteristics were examined more closely. Here, current and previous year's borer attacks and predation rate were deter mined on the bottom 12 m of all trees, in cluding sample trees. Trees were checked at least twice weekly during May through September of the additional year. Data col lection proceeded as described above. Ad ditionally, borer survival to the pupal stage was determined by checking for the pres ence of a well-defined adult emergence hole

Table 1. Summary of woodpecker predation rates on locust borers in 15 black locust stands in western Maryland during May through Sept. 1987. Presented are the number of black locust trees sampled, number of active borer mines on the lower 3 m of each sample tree, and number and percentage of depredated borers.

Site Type/Stand No.	Variable	Successional Stage					
		Mixed Forest	Forest-clone Edge	Clonal Growth	Clone-open Edge	Open Growth	Total
Old Field	No. Trees	24	30	20	20	20	134
	No. Borers	167	148	98	103	82	598
	No. Depredated	0	0	0	2	0	2
Pasture	No. Trees	20	20	30	28	16	114
	No. Borers	32	72	118	103	39	364
	No. Depredated	0	0	0	0	0	0
Opening	No. Trees	28	30	10	NP	NP	68
	No. Borers	124	148	81	NP	NP	353
	No. Depredated	0	1	0	NP	NP	1
Roadside	No. Trees	30	19	18	14	NP	81
	No. Borers	100	175	139	145	NP	559
	No. Depredated	8	6	1	0	NP	15
Strip mine	No. Trees	23	30	29	21	21	124
	No. Borers	119	260	328	239	211	1,157
	No. Depredated	0	0	0	3	8	11
Total	No. Trees	125	129	107	83	57	489
	No. Borers	542	803	764	590	332	2,679
	No. Depredated	8	7	7	6	8	30

> 4 mm in diameter in mid- through late July. A hole < 4 mm diameter indicated that a larva had died while small, probably prior to the pupal stage (McCann 1992).

Occasionally, predation on locust borers was directly observed. Data recorded during these incidental observations included the species, sex and, if possible, age (hatch year or after-hatch year) of the bird, and time required to extract the borer. Only hairy woodpeckers were observed in the act of predation.

Statistical analyses.—Using RD3 data, t-tests (for numeric variables) and chi-square tests (for categorical variables) were used to compare trees with versus without predation and depredated versus nondepredated mines (Sokal and Rohlf 1995). Relationships between incidence of predation, borer density, and tree characteristics were examined with Spearman's rank correlation test. Data were checked for normality and homoscedascity using a Kolmogorov-Smir-

nov test and Bartlett Box test, respectively. Means ± 1 standard deviation are reported. All statistical tests were considered significant if $P \leq 0.05$.

RESULTS

Overall predation rate.—A total of 2,629 active borer mines were monitored for bird predation. One or more mines were present on the bottom 3 m of 428 (87%) of 489 sample trees; no borers occurred in 61 trees (Table 1). The mean (±SD) number of mines per tree was 6.9 ± 8.4 (range, 0–64) and mines per stand ranged from 2.9 to 17.5.

Based on sample tree data, the overall predation rate in 1987 was only 1.01% (30 of 2,629 borers Table 1). No predation occurred in 9 stands. Among the other 6 stands, the predation rate ranged from 0.7 % (2 of 293 borers) through 1.7% (1 of 59 borers) except for one of the roadside stands (RD3), where 11.0% (14 of 127) of

Table 2. Summary of data on locust borer populations and woodpecker predation rate (bases on surveys of lower 12 m of all trees) in Roadside Stand no. 3 (RD3), western Maryland, during 1987 and 1988.

Variable	1987	1988	Both Years
No. active borer mines	627	397	1,024
No. depredated borers	108	94	202
Predation rate (%)	17.2	23.8	19.9
No. trees	46	32	78
No. trees with active borer mines	44	30	74
No. trees with depredated borers	26	20	46
Mean ($\pm$ SD) no. active borer mines per tree	13.6 (8.7)	12.4 (11.0)	13.1 (9.6)
Mean ($\pm$ SD) no. depredated borers per tree	2.5 (2.7)	3.0 (3.3)	2.7 (2.9)
Mean ($\pm$ SD) percentage of borers depredated per tree	15.3 (16.8)	22.1 (23.4)	18.0 (19.8)
Mean ($\pm$ SD) no. depredated borers per tree with ≥ 1 instance of predation	4.2 (2.4)	4.7 (2.9)	4.4 (2.6)

the borers in sample trees were depredated. There was little consistent variation in pre- dation rate among site categories (range = 0–2.9%) although successional stages av- eraged higher due to one strip-mine stand (open growth, 12.8%) (range = 0.3–2.7%).

During complete stand surveys, we found a total of 304 instances of avian pre- dation in 13 of the 15 stands. Approxi- mately 36% (108 borers) of this predation occurred in RD3. Predation was not restrict- ed to a particular habitat or successional stage. However, in a few stands and site types, the number of woodpecker attacks was relatively high in certain successional stages; e.g., 94.1% of the predation in strip mine sites occurred in either clone-open or open growth. One of the strip-mine stands, open growth stage, had 12.8% bird preda- tion rate, the highest for any single stand. Strip mines had notably greater numbers of borers per tree than the other site types (9.3 versus 6.9 for roadsides and 4.4 for old fields); this feature has been confirmed in other regional investigations (Harman et al. 1985b, 1989)

Predation rate in RD3.—Stand RD3 con- tained a total of 1024 active mines and bor- ers occurred in all but 2 trees during each year (Table 2). Borer density averaged 13.1 ($\pm$ 9.6) active mines per tree (bottom 12 m) but varied considerably (range = 1.47). The borer infestation level in RD3 was moder- ate and not statistically different ($P \geq 0.1$)

from that in other stands.The predation rate in RD3 during the first year was 19.9%, which, compared to other stands, was ex- ceptionally high. A greater percentage (X^2 = 6.05, 1 *df*, $P = 0.014$) of borers was dep- redated during the second year than the first (23.8% versus 17.2%). However, there were no interyear differences in borer density (*t* = 0.51, 76 *df*, $P = 0.61$) or in the percent- age of trees with active mines ($X^2 = 0.14$, 1 *df*, $P = 0.71$). The highest number of dep- redated borers found in a tree during a sin- gle year was 11 (of 15 borers) and the per- centage of mines depredated per tree ranged from 5.6% (1 of 18 borers) to 75.0% (6 of 8 borers).

Predation phenology and success.—We found no evidence of predation during the egg, overwintering larval, or early spring larval stages. Most instances of predation occurred in July and August (29 versus 17%, respectively), when later-instar larvae and pupae were present. In RD3, where pre- dation was monitored on a weekly basis during the second year, the number of avian attacks peaked during the third week of July, just before pupation when larvae at- tained maximum size and were most active. Predatory attempts per week for the six weeks from June 2–August 1, 1988, were 16, 21, 19, 27, 9, and 2.

Not all predatory entries into borer mines were successful, indicating that the borer larvae may have evaded the intrusion or the

Table 3. Comparison of black locust trees with and without woodpecker depredated locust borer mines in roadside stand no. 3 (RD3), western Maryland.

Variable	Year	Trees with Predation[a]			Trees without Predation[b]			P[c]
		Mean	SD	Range	Mean	SD	Range	
Dbh (cm)	1987	11.9	2.3	7.6–18.3	14.5	3.7	6.1–19.7	0.013
	1988	12.2	2.6	8.6–18.3	15.3	2.4	12.7–18.8	0.003
	Both	12.0	2.4	8.6–18.3	14.8	3.3	6.1–19.7	<0.001
Tree height (m)	1987	10.1	2.1	7.9–18.0	12.5	32	7.7–18.6	<0.001
	1988	10.5	2.4	7.8–18.0	12.6	2.4	10.1–15.9	0.032
	Both	10.3	2.2	7.9–18.0	12.8	2.9	7.7–18.6	<0.001
No. larvae per tree	1987	18.0	8.3	4–32	8.9[d]	5.2	1–20	<0.001
	1988	17.5	10.8	4–47	4 7	3.9	1–11	<0.001
	Both	17.8	9.3	4–47	7.4	5.1	1–20	<0.001
No. pupae per tree	1988	6.5	4 3	1–19	1.1	1.0	1–3	<0.001
Larval survivorship to pupal stage (%)	1988	38.4	13.9	12.5–66.7	28.2	30.4	0–100	0.335

[a] Sample sizes were 26, 20, and 46 for 1987, 1988, and both years combined, respectively.

[b] Sample sizes were 18, 10, and 28 for 1987, 1988, and both years combined, respectively.

[c] P-values are based on t-tests.

[d] Means were different ($P \leq 0.05$) between years based on t-tests.

Table 4. Spearman's rank correlations[a] between black locust tree characteristics and the incidence of woodpecker predation on locust borers in roadside stand no. 3 (RD3), western Maryland.

Variable	Year	Depredated Borers/Tree	
		Number	Percent
Dbh	1987	−0.389	−0.457
	1988	−0.503	−0.662
	Both	−0.460	−0.587
Tree height	1987	−0.408	−0.482
	1988	−0.462	−0.582
	Both	−0.439	−0.482
Crown class	1987	−0.211	−0.226
	1988	−0.394	−0.657
	Both	−0.330	−0.226
No. larvae per tree	1987	0.841	0.318
	1988	0.748	0.379
	Both	0.663	0.318
No. pupae per tree	1988	0.849	0.374
Larval survivorship to pupal stage	1988	0.314	0.175

[a] Spearman's rank correlation coefficients are shown. Using a 2-tailed test of significance, * $P \leq 0.05$, ** $P < 0.01$. Sample sizes were: 1987 = 44, 1988 = 30, both years = 74.

predator may have missed its target. In RD3, borers survived to the adult stage in 8.4% of depredated mines (17 of 202), while in other stands the survival rate was significantly higher at 16.5% ($X^2 = 5.77$; 1 df; $P \leq 0.05$).

Some dimensional and vigor aspects of trees were associated with frequency of bird predation. In RD3, trees with predation were significantly smaller than trees without predation in terms of dbh, height, and of less thrifty crown class (Table 3). Correlation analyses revealed that both the number of depredated mines per tree and the percentage of borers depredated per tree were inversely related to dbh, tree height and crown class (Table 4). Predation was also also positively correlated with larval and pupal density. There were no significant correlations in RD3 between borer density, borer survivorship, tree size, or crown class.

Significant differences also existed between the characteristics of depredated and nondepredated borer mines. Depredated ones were at greater heights, relative heights (height above ground divided by

Table 5. Comparison of woodpecker depredated and nondepredated locust borer mines in roadside stand #3 (RD3), western Maryland.

Variable	Year	Depredated Mines[a]			Nondepredated Mines[b]			P
		Mean	SD	Range	Mean	SD	Range	
Height above ground (m)[c]	1987	4.3	2.3	0.6–11.1	3.1[d]	2.0	0.1–9.4	<0.001
	1988	4.6	2.5	0.4–10.6	3.5	2.3	0.1–10.1	<0.001
	Both	4.5	2.4	0.4–11.1	3.2	2.1	0.1–10.1	<0.001
Relative height above ground[c]	1987	0.44	0.22	0.06–0.98	0.29[d]	0.19	0.01–0.91	<0.001
	1988	0.47	0.24	0.04–0.92	0.32	0.21	0.01–0.89	<0.001
	Both	0.46	0.23	0.04–0.98	0.30	0.20	0.01–0.91	<0.001
Stem diameter (cm)[c]	1987	9.1	2.9	2.8–17.0	11.4	3.1	3.8–21.0	<0.001
	1988	8.9	3.2	2.5–16.0	11.3	3.1	3.8–21.0	<0.001
	Both	9.0	3.0	2.5–17.0	11.4	3.1	3.8–21.0	<0.001
% in branches (vs. main bole)[e]	1987	5.6			1.2			<0.001
	1988	7.5			0			<0.001
	Both	6.4			0.8			<0.001
% with north (vs. south) orientation[e]	1987	0.36			51.2			0.005
	1988	48.4			53.3			0.406
	Both	41.8			52.0			0.011

[a] Sample sizes were 26, 20, and 48 for 1987, 1988, and both years combined, respectively.

[b] Sample sizes were 18, 10, and 28 for 1987, 1988, and both years combined, respectively.

[c] P-values based on t-tests.

[d] Means were different ($P \leq 0.05$) between years.

[e] P-values are based on chi-square tests.

tree height), and in smaller diameter stems, as shown in (Table 5), which provides data from the RD3 stand only. These predation data were taken to a height of 12 m. In contrast, previous studies have shown lower borer density in higher tree portions (Harman and Harman 1990). Also, combining study years, more borers were depredated on the south than north-facing side of stems (Table 5). Only 19 (1.9%) of the 1,024 active borer mines in RD3 occurred in branches; however, few branches existed below 12 m in this stand due to heavy shading and natural pruning. Branch mines were depredated at a higher n rate (68.4%) than mines along the main bole (18.8%), perhaps again reflecting a tendency by the birds to attack mines at relatively greater heights and in small diameter stems.

In stands other than RD3, the low incidence of predation in sample trees precluded most meaningful statistical comparisons. However, data collected during the complete stand surveys suggest that predators foraged on trees with similar characteristics as in RD3. For example, trees with predatory attacks tended to be relatively small (9.0 ± 4.3 cm dbh, range = 2.0 to 21.3) and 7.8 ± 3.4 m tall (range = 2.0 to 18.0). Over 75% of the trees with predation were less than 11.7 cm dbh and 10.1 m tall, and most were in the intermediate and suppressed crown classes. Complete stand survey data also show that depredated mines were located in relatively small diameter stems (mean = 4.5 ± 2.8 cm) and over 95% of all woodpecker attacks were in stems less than 10.2 cm diameter. The smallest diameter stem with predation was 1.3 cm, corresponding with the minimum stem size in which locust borers reside. No predation was recorded in stems over 17.8 cm diameter although borers commonly tunnel in stems as large as 38 cm. The mean depredated mine height was 3.9 ± 2.2 m and, unlike RD3, most woodpecker attacks (67.3%) occurred in branches rather than in the main bole. Woodpecker excavations

were usually conical shaped and oriented lengthwise along the branch or tree trunk. They measured, on average, 2.4 ($\pm$ 0.9) cm long (range = 0.7–8.1) by 1.6 ($\pm$ 0.6) cm wide (range = 0.5–3.6), and 1.6 ($\pm$ 0.6) cm deep (range = 0.4–3.3). These dimensions were each correlated with stem diameter ($R \geq 0.67$, $P < 0.001$).

Direct observations.—Thirty-six instances of predation were directly observed. Adult hairy woodpeckers *P. vilosus* (26 ♂, 2 ♀) accounted for 28 instances, six were by adult downy woodpeckers (*P. pubescens*) (4 ♂, 2 ♀), and two were by adult pileated woodpeckers *D. pileatus* (1 ♂, 1 ♀). In RD3, all direct observations (n = 17) were of adult male hairy woodpeckers.

No predation was observed by northern flickers (*Colaptes auratus* Linnaeus) or red-bellied woodpeckers (*Melaneupes carolnus* Linnaeus), although both species nest throughout the study area. A number of other species, including white-breasted nuthatches *Sitta carolinensus* Latham, brown creepers (*Certhia familiaris* Bonaparte), and black-and white warblers (*Miniotilta varia* Linnaeus), have morphological and behavioral adaptations for tree-trunk foraging (Jackson 1979), and could be potential predators of borer larvae. Although our actual observations included only woodpeckers, these and other avian species should be included as possible foragers in some of the instances of past predation, which could not be definitely assigned to woodpeckers. Predation by hairy woodpeckers occurred in a variety of successional stages and site types, while pileated and downy woodpecker predation was observed only in mature forest and young open or clonal growth, respectively.

DISCUSSION

The scope of the sample for site type comparison was influenced by sampling on the bottom 3 m branches and stem portions, and numerical comparisons from these analyses apply to this lower portion rather than to the entire tree. Other parts of the

study were not restricted to the bottom 3 m, and data were taken higher in the trees (i.e., 12 m for the roadside 3 stand, and unspecified height for direct observation with binoculars). The 3 m limit was necessary to facilitate the close viewing and evaluation of a large tree sample by an observor standing on the ground holding delicate equipment, and easily accessing all sides of the trees. Prior observations indicated that, in stands of this size, sufficient borer activity occurs below 3 m on trunks to allow valid comparisons. Sampling below 3 m, however, could cause data inferences to be influenced by such factors branch height, and/ or comparative visibility of the features in question.

With a few exceptions, avian predation appeared to exert only minor mortality in this study. These findings concur with casual observations by other authors who reported little (3–7% larval mortality) or no avian predation on locust borers (Garman 1916, Van Tyne 1983, Bourne 1986). Hall (1942), however, believed that woodpeckers are capable of causing much greater mortality (30–40% of locust borer larvae) and, as in our study, described heavier predation usually occurring in small, localized areas. Hall's studies were conducted in Ohio, away from the optimal range for black locust, where black locust growth is less thrifty, and pressure from the locust borer more intense than in the Appalachian Plateau.

The response of a predator population to changes in prey abundance has been described as consisting of two components: a numerical and functional response (Holling 1959). We attribute the low incidence of avian attacks on locust borers to a variety of factors that limited both types of responses. Although birds, particularly woodpeckers, are capable of strong numerical responses to increases in prey density, especially through aggregation behavior, such as occurs during bark beetle (*Dendroctonus* sp.) outbreaks (Blackford 1955, Baldwin 1960, Koplin 1969), locust borer numbers

are probably too low to elicit woodpecker aggregation behavior, even during severe infestations. Predation in our study oc curred during or just after the nesting sea son for hairy, downy, and pileated woodpeckers (Stewart and Robbins 1958), when their concentrations are limited by territorial behavior. Hutchinson (1951) and Yeager (1955) observed woodpecker feeding aggregations in areas where bark beetle out breaks exceeded 4 million larvae per ha and extended over thousands of hectares. Lo cust borers rarely reach even 1% of this density and the size of an infestation is ul timately limited by the availability of black locust trees, which typically are scattered or in small stands of less than 4 ha.

The overall predation rate appeared low compared to other wood-borer species, with similar-sized larvae, which have ranged from 9 to 39% for the red oak borer *Ena- phalodes rufulus* Haldeman (Hay 1972, Pet it et al. 1988, respectively), 67% for the oak branch borer *Goes debilis* LeConte (Solo mon 1977), and as high as 81% for the ash borer *Podosesia syringae* (Harris) (Solomon 1975). However, there are major dif ferences, such as the fact that these wood borers have 2–4 year life cycles and over winter as large, late-instar larvae and pupae with considerable energy value to preda tors. With these species, most bird preda tion occurs during fall and winter, and the predation rates reported were much higher than for locust borers (Solomon 1969, 1975, 1977; Hay 1972; Petit et al. 1988).

Predation may also be limited function ally by a combination of factors in addition to those named above. Downy, hairy and, to a lesser degree, pileated woodpeckers feed opportunistically on a variety of food resources, reducing the likelihood of con centrated foraging on a single prey species over an extended period of time (Beal 1911, Bent 1939, Lawrence 1966, Conner 1980). Each species also exhibits significant sea sonal differences in diet and foraging be havior (Jackson 1970; Conner 1979, 1981). In late spring and summer, deep-wood in sect prey such as wood-borers represent a relatively minor component of their diet. During fall and winter, the three species feed much more extensively on subcambial prey but locust borer larvae are extremely small at that time, measuring only about 2 mm long, and their oval galleries are only ~5 mm in diameter.

Habitat conditions in many sections of the stands also may have limited wood pecker predation. At least three (open, clone-open edge, and clonal) of the five black locust successional stages contained marginal or unsuitable foraging habitats for hairy and pileated woodpeckers, which pre fer older forest conditions and larger di ameter trees and branches as foraging sub strates (Bent 1939, Hoyt 1957, Kisiel 1972, Conner and Crawford 1974, Conner 1980, Renken and Wiggers 1989). Although downy woodpeckers feed in a variety of forest successional stages and on relatively small diameter stems (Bent 1939, Jackson 1970, Kisiel 1972, Williams 1975, Conner 1980), subcambial prey represent a minor component of their diet, especially during spring and summer (Conner 1980, 1981). Downy woodpeckers are also physically less capable of excavating deep-wood prey due to their relatively small bill, short tongue, and less developed head and neck musculature (Selander 1966, Lawrence 1966). We attributed most predation to hairy woodpeckers based, in part, on direct observations and the size and shape of woodpecker excavations. This species ac counted for over 75% of all direct obser vations of predation and all directly ob served predation in RD3. Although hairy woodpeckers prefer more mature forest conditions and larger diameter stems, they frequently forage in sapling and pole stage forests (Kisiel 1972, Conner 1980). This species also is a more capable excavator than downy woodpeckers (Selander 1966, Lawrence 1966) and feeds more frequently on subcambial prey during spring and sum mer (Selander 1966, Lawrence 1966, Con ner 1981).

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Other factors act against avian predation of locust borers, such as the relatively short period of availability of late larval and pupal stages, and certain characteristics of black locust wood, which is among the hardest of any tree species in eastern North America (Roach 1958). Also present are thorns, especially on smaller diameter stems and tree trunks where locust borer densities also may be greatest (McCann 1992). The thorns may impede woodpecker movement along the bark surface and reduce overall use of black locust trees as foraging substrates. Bark features of other tree species (e.g., honeylocust, *Gleditsia triacanthos* Linnaeus), thorns, and bark shingles of shagbark hickory, *Carya ovata* (Mill.) K. Koch, can have a similar effect on woodpecker foraging (Jackson 1970, 1979). Locust borers in their late larval and pupal stages, when their size might justify a predatory attempt, are not near the stem surface, but often relatively deep beneath the surface.

Reasons for the relatively high predation rate (19.9%) in RD3 were not apparent, but this area appeared isolated and localized. Numerous factors could be involved, including woodpecker densities and habitat, fluctuations of alternate prey, and possible alterations in borer behavior. One such observation was reported by Hall (1942) during a drought year in Ohio, in which larvae tended to remain in subcortical cavities rather than exhibit the normal habit of constructing tunnels; this would place larger larvae and pupae nearer the surface and more vulnerable to predation.

Predation rate was correlated with crown class, and with compass direction, with higher instances of predation on south than north facing stem surfaces. Black locust is very shade-intolerant (Roach 1958) and increased shade is usually seen with downward progression from dominant to suppressed crown class, accompanied by increasing decline and greater susceptibility to insects and fungi. Locust borer attack rates have also been found to increase with

increased percent of black locust in the stand (Harman et al. 1985a). Predation may respond due to increased borer infestation rates and aggregation of other invertebrates around wound entrances (McCann 1992).

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